

Swimmer-microrheology

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We discuss a locomotion of a three-sphere microswimmer in a viscoelastic medium and propose a new type of active microrheology. We derive a relation which connects average swimming velocity and frequency-dependent viscosity of the surrounding medium. In this relation, the viscous contribution can exist only when the time-reversal symmetry is broken, whereas the elastic contribution is present only when the structural symmetry of the swimmer is broken. The Purcell's scallop theorem breaks down for a three-sphere swimmer in a viscoelastic medium.

Microrheology is one of the most useful techniques to measure rheological properties of soft matter and various biological materials including cells [1, 2]. There are two different methods; passive microrheology and active microrheology. In the passive microrheology, both local and bulk mechanical properties of a medium can be extracted from a Brownian motion of a probe particle [3, 4]. In this method, the generalized Stokes-Einstein relation (GSER) is used to analyze thermal diffusive motions. In the active microrheology, on the other hand, the probe is actively pulled through the fluid, with the aim of driving the medium out-of-equilibrium and measuring mechanical responses [5, 6]. Within the linear response theory, the generalized Stokes relation (GSR) is employed to obtain the frequency-dependent complex shear modulus.

In this Letter, we propose a new type of active microrheology using a microswimmer. Microswimmers are tiny machines that swim in a fluid like sperm cells or motile bacteria, and are expected to be applied to microfluidics or microsystems [7]. As one of the simplest microswimmers, we consider Najafi-Golestanian's three-sphere swimmer model [8, 9], where three in-line spheres are linked by two arms of varying length (see Fig. 1). Recently such a swimmer has been experimentally realized [10]. We investigate its motion in a general viscoelastic medium, and obtain a relation which connects the average swimming velocity and the frequency-dependent complex shear viscosity of the surrounding viscoelastic medium. We show explicitly that the absence of the time-reversal symmetry of the swimmer motion leads to the real part of the viscosity, whereas the absence of the structural symmetry of the swimmer is reflected in the imaginary part of the viscosity. Hence we call it as "swimmer-microrheology". Our result also indicates that the Purcell's scallop theorem [11, 12], which states that time-reversible body motion cannot be used for locomotion in a Newtonian fluid, breaks down for a three-sphere swimmer in viscoelastic media if the structural symmetry is violated.

The general equation that describes the hydrodynamics of low Reynolds number flow in a viscoelastic medium

is given by the following generalized Stokes equation [13]:

$$0 = \int_{-\infty}^t dt' \eta(t-t') \nabla^2 \mathbf{v}(\mathbf{r}, t') - \nabla p(\mathbf{r}, t). \quad (1)$$

Here $\eta(t)$ is the time-dependent shear viscosity, \mathbf{v} is the velocity field, p is the pressure field, and \mathbf{r} stands for three-dimensional positional vector. The above equation is further subjected to the incompressibility condition, $\nabla \cdot \mathbf{v} = 0$. From these equations, one can obtain a linear relation between the time-dependent force $F(t)$ acting on a hard sphere of radius a and its time-dependent velocity $V(t)$. In the Fourier domain, it can be represented as

$$V(\omega) = \frac{1}{6\pi\eta[\omega]a} F(\omega), \quad (2)$$

where we use a bilateral Fourier transform for $V(\omega) = \int_{-\infty}^{\infty} dt V(t) e^{-i\omega t}$ and $F(\omega)$, while we employ a unilateral one for $\eta[\omega] = \int_0^{\infty} dt \eta(t) e^{-i\omega t}$. Equation (2) is the GSR that has been successfully used in active microrheology experiments [5], and its mathematical validity was also discussed before [6].

Next, we briefly explain the three-sphere model for a minimum swimmer introduced by Najafi and Golestanian [8, 9]. As schematically shown in Fig. 1, this model consists of three spheres of the same radius a that are connected by two arms of lengths $L_1(t)$ and $L_2(t)$ which undergo time-dependent motions. Their explicit time dependencies will be given later. If we define the velocity of each sphere along the swimmer axis as $V_i(t)$ with

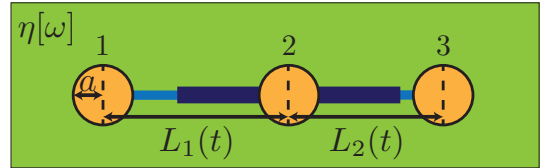


FIG. 1. The Najafi-Golestanian's three-sphere swimmer model. Three identical spheres of radius a are connected by arms of lengths $L_1(t)$ and $L_2(t)$ and undergo time-dependent cyclic motions. The swimmer is embedded in a viscoelastic medium characterized by a frequency-dependent complex shear viscosity $\eta[\omega]$.

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$i = 1, 2, 3$, we have

$$\dot{L}_1(t) = V_2(t) - V_1(t), \quad (3)$$

$$\dot{L}_2(t) = V_3(t) - V_2(t), \quad (4)$$

where \dot{L}_1 and \dot{L}_2 indicate the time derivatives.

Due to the hydrodynamic effect, each sphere exerts a

force F_i on the viscoelastic medium and experiences a force $-F_i$ from it. To relate the forces and the velocities in the frequency domain, we use the GSR in Eq. (2) and the Oseen tensor in which the frequency-dependent viscosity $\eta[\omega]$ is used instead of a constant one [3, 4]. Assuming that $a \ll L_1, L_2$, we can write [8, 9]

$$V_1(\omega) = \frac{F_1(\omega)}{6\pi\eta[\omega]a} + \frac{1}{4\pi\eta[\omega]} \frac{F_2(\omega) * L_1^{-1}(\omega)}{2\pi} + \frac{1}{4\pi\eta[\omega]} \frac{F_3(\omega) * (L_1 + L_2)^{-1}(\omega)}{2\pi}, \quad (5)$$

$$V_2(\omega) = \frac{1}{4\pi\eta[\omega]} \frac{F_1(\omega) * L_1^{-1}(\omega)}{2\pi} + \frac{F_2(\omega)}{6\pi\eta[\omega]a} + \frac{1}{4\pi\eta[\omega]} \frac{F_3(\omega) * L_2^{-1}(\omega)}{2\pi}, \quad (6)$$

$$V_3(\omega) = \frac{1}{4\pi\eta[\omega]} \frac{F_1(\omega) * (L_1 + L_2)^{-1}(\omega)}{2\pi} + \frac{1}{4\pi\eta[\omega]} \frac{F_2(\omega) * L_2^{-1}(\omega)}{2\pi} + \frac{F_3(\omega)}{6\pi\eta[\omega]a}, \quad (7)$$

where we have used the bilateral Fourier transform such as $L_1^{-1}(\omega) = \int_{-\infty}^{\infty} dt [L_1(t)]^{-1} e^{-i\omega t}$. Furthermore, the convolution of two functions are generally defined by $g_1(\omega) * g_2(\omega) = \int_{-\infty}^{\infty} d\omega' g_1(\omega - \omega') g_2(\omega')$ in the above equations.

As in the original study, we are interested in autonomous net locomotion of the swimmer, and there are no external forces acting on the spheres. If the inertia of the surrounding fluid can be neglected, we have the following force balance condition

$$F_1(t) + F_2(t) + F_3(t) = 0. \quad (8)$$

Since Eqs. (5)–(7) involve the convolutions in the frequency domain, we cannot solve these equations for arbitrary $L_1(t)$ and $L_2(t)$. Here we assume that the two arms undergo the following periodic motions:

$$L_1(t) = \ell + d_1 \cos(\Omega t), \quad (9)$$

$$L_2(t) = \ell + d_2 \cos(\Omega t - \phi). \quad (10)$$

In the above, ℓ is a constant length, d_1 and d_2 are amplitudes of the oscillatory motions, Ω is a common arm frequency, and ϕ is a mismatch in phases between the two arms. In the following analysis, we generally assume that $d_1, d_2 \ll \ell$. The *time-reversal symmetry* of the arm motion is present when $\phi = 0$ and π . Furthermore, we characterize the *structural symmetry* of the swimmer by d_1 and d_2 , i.e., the structure is symmetric when $d_1 = d_2$ while it is asymmetric when $d_1 \neq d_2$.

Since the arm frequency is Ω , we assume that the velocities and the forces of the three spheres can be generally

written as

$$V_i(\omega) = V_{i,0} \delta(\omega) + \sum_{n=1}^{\infty} [V_{i,n} \delta(\omega + n\Omega) + V_{i,-n} \delta(\omega - n\Omega)], \quad (11)$$

$$F_i(\omega) = F_{i,0} \delta(\omega) + \sum_{n=1}^{\infty} [F_{i,n} \delta(\omega + n\Omega) + F_{i,-n} \delta(\omega - n\Omega)], \quad (12)$$

where $i = 1, 2, 3$ for the three spheres. Substituting Eqs. (11) and (12) into the six coupled equations (3), (4), (5), (6), (7) and (8), we obtain a matrix equation with infinite dimensions.

Under the conditions $d_1, d_2 \ll \ell$ and $a \ll \ell$, we are allowed to consider only $n = -1, 0, 1$ and further approximate as $F_{i,\pm 2} \approx 0$. Then we can solve for six unknown functions $V_i(\omega)$ and $F_i(\omega)$, and further calculate the total swimming velocity $V = (V_1 + V_2 + V_3)/3$. Up to the lowest order terms in a , the average swimming velocity over one cycle of motion becomes [14]

$$\bar{V} \approx \frac{7d_1 d_2 a \Omega}{24\ell^2} \frac{\eta'[\Omega]}{\eta_0} \sin \phi - \frac{5(d_1^2 - d_2^2) a \Omega}{48\ell^2} \frac{\eta''[\Omega]}{\eta_0}, \quad (13)$$

where $\eta'[\Omega]$ and $\eta''[\Omega]$ are the real and the imaginary parts of the complex shear viscosity, respectively, and $\eta_0 = \eta[\Omega \rightarrow 0]$ is a constant zero-frequency viscosity.

The first term in Eq. (13) can be regarded as a viscous contribution and is present only if the time-reversal symmetry of the swimmer motion is broken, i.e., $\phi \neq 0, \pi$. The second term, on the other hand, corresponds to an elastic contribution, and exists only when the structural symmetry of the swimmer is broken, i.e., $d_1 \neq d_2$. If we were able to control d_1 , d_2 and Ω of the swimmer, we first obtain $\eta'[\Omega]$ by measuring \bar{V} as a function of Ω by setting $d_1 = d_2$. Then we differentiate between d_1

TABLE I. Locomotion of a three-sphere swimmer in a viscoelastic medium and the relevant rheological information.

medium	viscous		viscoelastic			
time-reversal symmetry	Y	N	Y	N	Y	N
structural symmetry	Y	N	Y	N	Y	N
swimmer motion	N	N	Y	Y	N	Y
rheological information	—	—	N	N	—	η'' , η' , η' , η''

and d_2 to see the change in \bar{V} , which then yields $\eta''[\Omega]$. The corresponding complex shear modulus is simply obtained by $G[\Omega] = i\Omega\eta[\Omega]$. This is a new type of active microrheology that we propose in this Letter.

For a purely Newtonian fluid, namely, for a medium characterized by a constant viscosity, the second term in Eq. (13) vanishes, and the first term coincides with the expression obtained by Golestanian and Ajdari [9]. It should be noticed here, however, that the velocity \bar{V} in this case no longer depends on the constant viscosity (because $\eta'[\Omega]/\eta_0 = 1$) and we cannot measure it by looking at \bar{V} . Equation (13) also implies that the swimmer cannot move in a purely elastic medium for which we have $\eta_0 \rightarrow \infty$. Importantly, due to the presence of the second term, Purcell's scallop theorem breaks down for a three-sphere swimmer in a viscoelastic medium. Namely, even if the time-reversal symmetry of the swimmer motion is not broken, i.e., $\phi = 0, \pi$, the present swimmer can still move in a viscoelastic medium due to the second term as long as its structural symmetry is broken, i.e., $d_1 \neq d_2$. According to Eq. (13), the motion of a three-sphere swimmer in a viscoelastic medium and the relevant rheological information are summarized in Table I.

To further illustrate our result, we first assume that the surrounding viscoelastic medium is described by a simple Maxwell model. In this case, the frequency-dependent viscosity can be written as

$$\eta[\omega] = \eta_0 \frac{1 - i\omega\tau_M}{1 + \omega^2\tau_M^2}, \quad (14)$$

where τ_M is the characteristic time scale. Within this model, the medium behaves as a viscous fluid for $\omega\tau_M \ll 1$, while it becomes elastic for $\omega\tau_M \gg 1$. Using Eq. (14), we can easily obtain the average swimming velocity in Eq. (13) as

$$\begin{aligned} \bar{V} = & \frac{7d_1d_2a\Omega}{24\ell^2} \frac{1}{1 + \Omega^2\tau_M^2} \sin\phi \\ & + \frac{5(d_1^2 - d_2^2)a\Omega}{48\ell^2} \frac{\Omega\tau_M}{1 + \Omega^2\tau_M^2}. \end{aligned} \quad (15)$$

The first viscous term increases as $\bar{V} \sim \Omega$ for $\Omega\tau_M \ll 1$, while it decreases as $\bar{V} \sim \Omega^{-1}$ for $\Omega\tau_M \gg 1$. This is a unique feature of the viscoelasticity [7, 15, 16], but such a reduction occurs simply because the medium responds elastically in the high-frequency regime. On the other

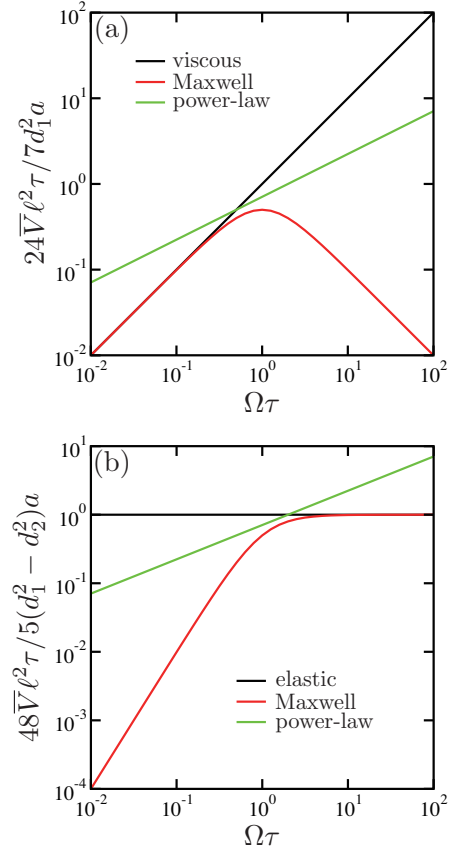


FIG. 2. The average swimming velocity \bar{V} as a function of $\Omega\tau$ where Ω is the arm frequency and τ represents either τ_M for a Maxwell fluid (red lines) or τ_p for a power-law fluid (green lines). In the power-law model, we choose $\alpha = 1/2$. (a) The viscous contribution by setting $\phi = \pi/2$ and $d_1 = d_2$. Here \bar{V} is scaled by $7d_1^2a/(24\ell^2\tau)$. The case for a viscous fluid is plotted by the black line. (b) The elastic contribution by setting $\phi = 0$ and $d_1 \neq d_2$. Here \bar{V} is scaled by $5(d_1^2 - d_2^2)a/(48\ell^2\tau)$. The case for an elastic medium is plotted by the black line.

hand, the second elastic term increases as $\bar{V} \sim \Omega^2$ for $\Omega\tau_M \ll 1$, and it approaches a constant for $\Omega\tau_M \gg 1$. In Fig. 2(a), we plot the average swimming velocity \bar{V} as a function of the dimensionless arm frequency $\Omega\tau_M$ when $\phi = \pi/2$ and $d_1 = d_2$. This plot corresponds to the first term in Eq. (15). As a reference, the behavior of $\bar{V} \sim \Omega$ for a purely viscous fluid is also plotted. Figure 2(b) is a similar plot when $\phi = 0$ and $d_1 \neq d_2$, and corresponds to the second term in Eq. (15).

As a different example, we next consider the case in which the viscoelastic medium is described by a power-law model such that [13, 17, 18]

$$\eta[\omega] = G_0(i\omega)^\alpha, \quad (16)$$

where the exponent can take values $0 \leq \alpha \leq 1$. With this expression, the complex shear modulus also obeys a power-law behavior, $G[\omega] = G_0(i\omega)^\alpha$. The limits of

$\alpha = 0$ and 1 correspond to the purely elastic and the purely viscous cases, respectively. In the case of a power-law fluid, the average swimming velocity can be obtained from Eqs. (13) and (16) as

$$\begin{aligned} \bar{V} = & \frac{7d_1d_2a}{24\ell^2\tau_p}(\Omega\tau_p)^\alpha \sin(\pi\alpha/2) \sin\phi \\ & + \frac{5(d_1^2 - d_2^2)a}{48\ell^2\tau_p}(\Omega\tau_p)^\alpha \cos(\pi\alpha/2), \end{aligned} \quad (17)$$

where $\tau_p = (\eta_0/G_0)^{1/(1-\alpha)}$. Here we have assumed that the medium behaves as a purely viscous fluid in the low-frequency limit characterized by a finite viscosity η_0 . According to the above expression, the swimming velocity scales as $\bar{V} \sim \Omega^\alpha$ both in the first and the second terms. For the purely viscous case of $\alpha = 1$, the first term reduces to the result by Golestanian and Ajdari [9], while the second term vanishes. For the purely elastic case of $\alpha = 0$, on the other hand, the first term vanishes and the second term remains although the latter does not depend on the arm frequency Ω any more. In Figs. 2(a) and (b), we have also plotted the average velocity \bar{V} as a function $\Omega\tau_p$ when $\alpha = 1/2$. In both of these plots, the scaling behavior $\bar{V} \sim \Omega^{1/2}$ is seen.

Lauga considered an axisymmetric squirming motion of a sphere (squirmer) embedded in an Oldroyd-B fluid which typically represents a polymeric fluid [19]. He reported that the scallop theorem in a viscoelastic fluid breaks down if the squirmer has a fore-aft asymmetry in its surface velocity distribution. For a time-reversal deformation given by a simple sinusoidal gait, he showed that the average swimming velocity is given by $\bar{V} \sim \Omega \text{De}/(1 + \text{De}^2)$, where the Deborah number is

given by $\text{De} = \Omega\tau_0$ with a characteristic relaxation time τ_0 in the Oldroyd-B model. Such a frequency dependence of the swimming velocity is identical to the second term of Eq. (15) obtained for a Maxwell fluid although Eq. (13) is more general. On the other hand, our result is different from that by Curtis and Gaffney [20], because they showed that the swimming velocity in a viscoelastic medium is the same as that in a Newtonian fluid.

To summarize, we have proposed a new active microrheology using the Najafi-Golestanian's three-sphere swimmer. The frequency dependence of the average swimming speed provides us with the complex shear viscosity of the surrounding viscoelastic medium. Here the viscous contribution can exist only when the time-reversal symmetry of the swimmer is broken, whereas the elastic contribution is present only if its structural symmetry is broken.

Even though the argument in this Letter is restricted to the artificial three-sphere swimmer, we expect that our basic concept can be still applied to more complex biological processes such as the motion of bacteria, the flagellated cellular swimming, or the beating of cilia. Since most of these phenomena take place in viscoelastic environment, we hope that the concept of our new active microrheology will be used in the future to reveal their mechanical and dynamical properties.

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- [1] T. M. Squires and T. G. Mason, *Annu. Rev. Fluid Mech.* **42**, 413 (2010).
 - [2] D. T. N. Chen, Q. Wen, P. A. Janmey, J. C. Crocker, and A. G. Yodh, *Annu. Rev. Condens. Matter Phys.* **1**, 301 (2010).
 - [3] T. G. Mason and D. A. Weitz, *Phys. Rev. Lett.* **74**, 1250 (1995).
 - [4] T. G. Mason, *Rheol. Acta* **39**, 371 (2000).
 - [5] F. Gittes, B. Schnurr, P. D. Olmsted, F. C. MacKintosh, and C. F. Schmidt, *Phys. Rev. Lett.* **79**, 3286 (1997).
 - [6] B. Schnurr, F. Gittes, F. C. MacKintosh, and C. F. Schmidt, *Macromolecules* **30**, 7781 (1997).
 - [7] E. Lauga and T. R. Powers, *Rep. Prog. Phys.* **72**, 096601(2009).
 - [8] A. Najafi and R. Golestanian, *Phys. Rev. E* **69**, 062901 (2004).
 - [9] R. Golestanian and A. Ajdari, *Phys. Rev. E* **77**, 036308 (2008).
 - [10] G. Grosjean, M. Hubert, G. Lagubeau, and N. Vande-walle, *Phys. Rev. E* **94**, 021101(R) (2016).
 - [11] E. M. Purcell, *Am. J. Phys.* **45**, 3 (1977).
 - [12] E. Lauga, *Soft Matter* **7**, 3060 (2011).
 - [13] R. Granek, *Soft Matter* **7**, 5281 (2011).
 - [14] (Supplemental material) The detailed derivation of Eq. (13) is provided online.
 - [15] H.C. Fu, T. R. Powers, and C. W. Wolgemuth, *Phys. Rev. Lett.* **99**, 258101 (2007).
 - [16] H. C. Fu, C. W. Wolgemuth, and T.R. Powers, *Phys. Fluids* **21**, 033102 (2009).
 - [17] S. Komura, S. Ramachandran, and K. Seki, *EPL* **97**, 68007 (2012).
 - [18] S. Komura, K. Yasuda, and R. Okamoto, *J. Phys.: Condens. Matter* **27**, 432001 (2015).
 - [19] E. Lauga, *EPL* **86**, 64001 (2009).
 - [20] M. P. Curtis and E. A. Gaffney, *Phys. Rev. E* **87**, 043006 (2013).

Supplemental Materials: Swimmer-microrheology

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In this Supplemental Materials, we show the detailed derivation of Eq. (13). Substituting Eqs. (9) and (11) into Eq. (3), we obtain

$$V_{2,0} - V_{1,0} = 0, \quad (S1)$$

$$V_{2,1} - V_{1,1} = -i\pi d_1 \Omega, \quad (S2)$$

$$V_{2,-1} - V_{1,-1} = i\pi d_1 \Omega, \quad (S3)$$

$$V_{2,n} - V_{1,n} = 0 \quad \text{for } |n| \geq 2. \quad (S4)$$

Similarly, substituting Eqs. (10) and (11) into Eq. (4), we obtain

$$V_{3,0} - V_{2,0} = 0, \quad (S5)$$

$$V_{3,1} - V_{2,1} = \pi d_2 \Phi_2 \Omega, \quad (S6)$$

$$V_{3,-1} - V_{2,-1} = \pi d_2 \Phi_1 \Omega, \quad (S7)$$

$$V_{3,n} - V_{2,n} = 0 \quad \text{for } |n| \geq 2, \quad (S8)$$

where we have used the following notations

$$\Phi_1 = i \cos \phi + \sin \phi, \quad (S9)$$

$$\Phi_2 = -i \cos \phi + \sin \phi. \quad (S10)$$

Next we expand Eqs. (5), (6) and (7) in terms of the small quantities d_1/ℓ and d_2/ℓ while keeping only the lowest order terms. Substituting Eqs. (11) and (12) into these three equations, we obtain

$$\begin{aligned} V_{1,n} \approx & \frac{F_{1,n}}{6\pi\eta[-n\Omega]a} + \frac{1}{4\pi\eta[-n\Omega]\ell} \left(F_{2,n} - \frac{d_1 F_{2,n+1}}{2\ell} - \frac{d_1 F_{2,n-1}}{2\ell} \right) \\ & + \frac{1}{4\pi\eta[-n\Omega]\ell} \left(\frac{F_{3,n}}{2} - \frac{d_1 F_{3,n+1}}{8\ell} - \frac{d_1 F_{3,n-1}}{8\ell} + \frac{id_2 \Phi_1 F_{3,n+1}}{8\ell} - \frac{id_2 \Phi_2 F_{3,n-1}}{8\ell} \right), \end{aligned} \quad (S11)$$

$$\begin{aligned} V_{2,n} \approx & \frac{1}{4\pi\eta[-n\Omega]\ell} \left(F_{1,n} - \frac{d_1 F_{1,n+1}}{2\ell} - \frac{d_1 F_{1,n-1}}{2\ell} \right) + \frac{F_{2,n}}{6\pi\eta[-n\Omega]a} \\ & + \frac{1}{4\pi\eta[-n\Omega]\ell} \left(F_{3,n} + \frac{id_2 \Phi_1 F_{3,n+1}}{2\ell} - \frac{id_2 \Phi_2 F_{3,n-1}}{2\ell} \right), \end{aligned} \quad (S12)$$

$$\begin{aligned} V_{3,n} \approx & \frac{1}{4\pi\eta[-n\Omega]\ell} \left(\frac{F_{1,n}}{2} - \frac{d_1 F_{1,n+1}}{8\ell} - \frac{d_1 F_{1,n-1}}{8\ell} + \frac{id_2 \Phi_1 F_{1,n+1}}{8\ell} - \frac{id_2 \Phi_2 F_{1,n-1}}{8\ell} \right) \\ & + \frac{1}{4\pi\eta[-n\Omega]\ell} \left(F_{2,n} + \frac{id_2 \Phi_1 F_{2,n+1}}{2\ell} - \frac{id_2 \Phi_2 F_{2,n-1}}{2\ell} \right) + \frac{F_{3,n}}{6\pi\eta[-n\Omega]a}. \end{aligned} \quad (S13)$$

Note that the couplings between different n -modes are involved in these equations. Finally, substituting Eq. (12) into Eq. (8), we obtain

$$F_{1,n} + F_{2,n} + F_{3,n} = 0. \quad (S14)$$

The above set of equations constitute a matrix equation with infinite dimensions and cannot be solved in general. Under the assumption of $a \ll \ell$, however, we are allowed to consider only $n = -1, 0, 1$ and further approximate as $F_{i,\pm 2} \approx 0$. The justification of the latter approximation is also seen by solving Eqs. (S4), (S8), (S11), (S12), (S13) and (S14) for $n = \pm 2$ and taking the limit of $a \ll \ell$. Hence the above set of equations can be solved for 18 unknowns, i.e., $V_{i,n}$ and $F_{i,n}$ for $i = 1, 2, 3$ and $n = -1, 0, 1$.

The velocity of each sphere is simply obtained by the inverse Fourier transform, $V_i(t) = (2\pi)^{-1} \int_{-\infty}^{\infty} d\omega V_i(\omega) e^{i\omega t}$. The average swimming velocity over one cycle of motion is then calculated by

$$\bar{V} = \frac{\Omega}{2\pi} \int_0^{2\pi/\Omega} dt [V_1(t) + V_2(t) + V_3(t)]/3. \quad (S15)$$

Up to the lowest order terms in a , we finally obtain Eq. (13). In order to obtain more accurate higher order terms in a , one needs to take into account the higher order n -modes ($|n| \geq 2$).